

On the Rat Trail in Near Oceania: Applying the Commensal Model to the Question of the Lapita Colonization¹

E. Matisoo-Smith,^{2,4,7} M. Hingston,^{3,4} G. Summerhayes,⁵ J. Robins,^{2,4} H. A. Ross,³ and M. Hendy⁶

Abstract: Presented here are the most recent results of our studies of *Rattus exulans*, one of the main commensal animals transported across the Pacific by Lapita peoples and their descendants. We sampled several locations in Near Oceania to determine distribution of *R. exulans* mitochondrial DNA (mtDNA) haplotypes in the region. We also obtained data regarding distribution of other introduced *Rattus* species to several islands in the Bismarck Archipelago. Our results suggest that there were multiple introductions of *R. exulans* to the region, which may suggest a more complex history for Lapita populations in Near Oceania.

ONE OF THE GREATEST impacts of human arrival on previously uninhabited islands is the introduction of human-associated plants and animals. The species introduced by humans can include not only intentional introductions such as domesticated plants and animals, but also a range of unintentionally transported species including weeds, insects, and other pests (Kirch 1982, Lee et al. 2007). Often island ecosystems contain a na-

ive fauna and numerous endemic species that cannot compete with the more recent introductions.

Despite the often negative impacts of introduced species on island ecosystems, there were clearly good reasons for people to transport their familiar plants and animals to the new environments they occupied. The transported landscapes (Kirch 1984) of Pacific peoples also provide a valuable resource for prehistorians. Not only do they allow us to understand and appreciate how humans adapted to the various environments they encountered, but understanding the history of the plants and animals that humans transported can provide direct evidence regarding the history of the humans themselves: Where did they come from and when? How many introductions and population arrivals were there? Is the appearance of a particular species associated with any particular archaeologically definable culture?

Beginning in the 1990s a program was developed at the University of Auckland focused on determining if tracking the movement of commensal animals introduced to Pacific islands by initial human colonists, through analyses of mitochondrial DNA (mtDNA) variation, might serve as a proxy for tracing human migration in the Pacific (Matisoo-Smith 1994, Matisoo-Smith et al. 1998). Pacific colonists transported, among other things, dogs, pigs, chickens, and rats when they settled the previously uninhabited islands of Remote Oceania. It is also gener-

¹ This research was funded by the Royal Society of New Zealand under Marsden Project UOA510: The Rat's Tale: Tracking Lapita Peoples through Phylogenetic Analyses of Pacific Rats. Manuscript accepted 23 January 2009.

² Department of Anthropology, University of Auckland, Auckland 1, New Zealand.

³ School of Biological Sciences, University of Auckland, Auckland 1, New Zealand.

⁴ Allan Wilson Centre for Molecular Ecology and Evolution, University of Auckland, Auckland 1, New Zealand.

⁵ Department of Anthropology, University of Otago, P.O. Box 56, Dunedin, Otago, New Zealand.

⁶ Allan Wilson Centre for Molecular Ecology and Evolution, Massey University, Palmerston North Campus, Private Bag 11222, Palmerston North 444, New Zealand.

⁷ Corresponding author (e-mail: e.matisoo-smith@auckland.ac.nz).

ally agreed that the Lapita colonists were the first to introduce dogs, pigs, chickens, and the Pacific rat (*Rattus exulans*) to islands in Near Oceania (Kirch 2000, Spriggs 1997), though debates continue around the possibility of earlier, pre-Lapita introductions of pigs and dogs to New Guinea (Bulmer 1982, 2001, Goreki et al. 1991, Allen 2000, Green 2000, Bellwood and White 2005, Larson et al. 2007).

It was decided, for a number of reasons, that the Pacific rat, *R. exulans*, was the best animal with which to first develop and test what we now refer to as the Commensal Model for human settlement of the Pacific. The Commensal Model is based on the close relationship between human populations and the plants and animals they transported across the Pacific. By identifying the genetic relationship of the various populations of commensal plants and animals, we can model the prehistoric migration and interaction patterns of Pacific peoples. A primary reason for the choice of *R. exulans* for a commensal study is its near-ubiquitous distribution in the Pacific. In addition, although the dogs, pigs, and chickens carried by early Pacific colonists belong to the same species as those brought in by European vessels from the 1700s onward, the rats introduced by these same historic vessels, *Rattus rattus* and *Rattus norvegicus*, are different species and do not interbreed with *R. exulans* (Mayr 2000, Robins et al. 2007). *Rattus exulans* is not known to stow away in European shipping vessels, and therefore the populations living on Pacific islands today are the direct descendants of those introduced by prehistoric colonists. We can therefore study extant populations as well as archaeological remains of *R. exulans* from across the Pacific to model the prehistoric human colonization of Remote Oceania.

The first major test of the Commensal Model for human settlement was based on an analysis of mtDNA variation in Polynesian populations of *R. exulans* (Matisoo-Smith 1994, Matisoo-Smith et al. 1998). Analyses of 132 *R. exulans* samples collected from throughout Polynesia indicated that the Commensal Model worked, with results suggesting that there were two major interaction

spheres in central East Polynesia (see Figure 1), both most likely originating in a homeland region centered in the southern Cook and Society islands. A southern interaction sphere connected these populations with New Zealand and the Kermadec Islands, and a northern interaction sphere connected this homeland region to the Marquesas and Hawaiian islands. These results were consistent with archaeological and linguistic data as well as oral traditions (Green 1966, Kirch 1986, Irwin 1992, Cachola-Abad 1993). Once it was shown that the Commensal Model did indeed provide a reasonable proxy for tracking human migrations, the range was expanded beyond the Polynesian triangle, and a diachronic perspective was added through the application of ancient DNA (aDNA) methods to archaeological remains of *R. exulans* (Matisoo-Smith et al. 1997, 1999, 2001).

To further expand this Commensal Model and address the issue of Lapita origins, Matisoo-Smith and Robins (2004) looked at how Polynesian and other Remote Oceanic samples related to those from Near Oceania and Island Southeast Asia. The results of these analyses identified three major haplogroups of *R. exulans*, each with a very distinct geographic distribution. All three haplogroups appeared to be ultimately derived from Mainland Southeast Asian populations. Haplogroup I was found only in populations from the Philippines, Borneo, and Sulawesi. Although its presence in Borneo may represent natural expansion of the species across the Sunda Shelf during periods of lowered sea levels, Haplogroup I was most likely transported by humans to both the Philippines and Sulawesi, which were separated from Sunda by deep undersea troughs. It was, however, the distribution of Haplogroups II and III that provided evidence of importance to issues of Lapita expansion. Given the archaeological evidence for a clear link between Lapita sites in Near and Remote Oceania, the results of this study were surprising. It was found that the Near and Remote Oceanic *R. exulans* populations sampled were very different. In fact, there were *no* Near Oceanic mtDNA lineages in Remote Oceania and vice versa, but both lineages

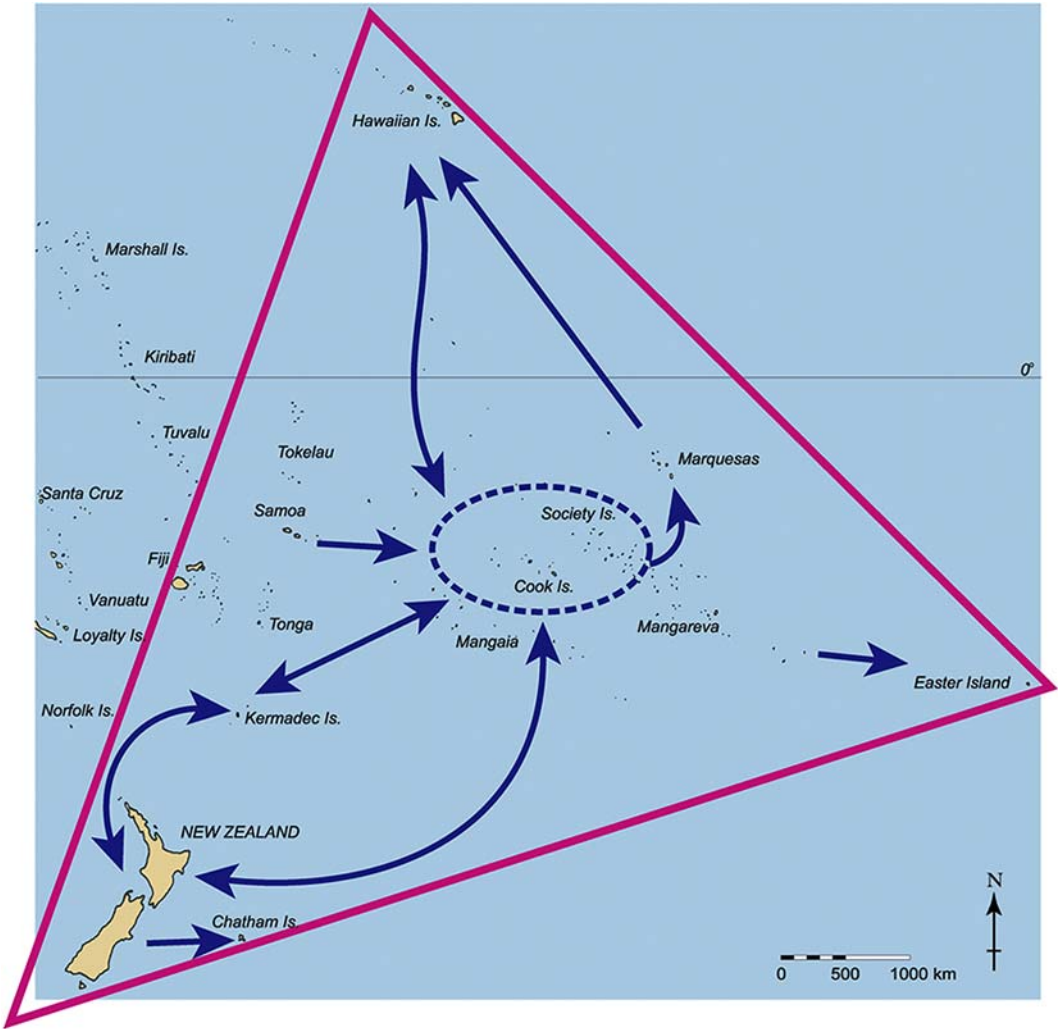


FIGURE 1. Map of Polynesia showing the interaction spheres identified through mtDNA analyses of Polynesian populations of *Rattus exulans*.

were present in Halmahera (Island Southeast Asia/Wallacea) to the west, where they were presumably introduced by humans at some point in prehistory. Studies of morphological variation of Pacific *R. exulans* (Tate 1935, Motokawa 2004) have reported a similar lack of continuity between Near and Remote Oceania. This could be (1) real; or (2) due to two introductions of *R. exulans* to Near Oceania—an early one to the main islands,

followed by a Lapita introduction to small islets, locations that have not been sampled in any previous analyses, morphological or genetic. Our goal was therefore to test these two possibilities through more thorough and specifically directed sampling of both modern and archaeological *R. exulans* populations from throughout Near Oceania.

Archaeological evidence suggests that the Lapita people generally targeted small, off-

shore islands for settlement, but the Near Oceanic *R. exulans* samples reported in Matisoo-Smith and Robins (2004) were primarily from larger islands (e.g., New Guinea, New Britain, and Bougainville), which were not typical early Lapita targets. *Rattus exulans* is generally assumed to be a Lapita introduction to both Near and Remote Oceania, yet the precise dating of its introduction to Near Oceania is problematic, because sites from the period just before Lapita arrival are rare. Three *R. exulans* bones were found at Panakiwuk, New Ireland, in layers dating to 8,000–13,000 B.P., but with such early dates, they were assumed to be there as a result of site disturbance (Marshall and Allen 1991). There is much evidence of animal translocation in the region from that period onward (Flannery 1995, Grayson 2001), so it is possible that *R. exulans* was introduced to Near Oceania before Lapita. If one lineage of *R. exulans* were introduced and established on the large islands earlier than 3,500 B.P. and Lapita peoples then introduced a new lineage to the previously uninhabited islands, then *R. exulans* from the smaller islets, like Mussau in the Bismarcks, should have Remote Oceanic lineages distinct from those found on the larger islands. If they do not, then Remote Oceanic *R. exulans* must be coming from elsewhere, and the settlement of the region is even more complex than we currently believe.

To address this question, we decided to undertake a major research project in Near Oceania. This project involved targeted fieldwork to trap extant samples of *R. exulans* from the more likely Lapita target locations such as the small islands in the Admiralty and St. Matthias island groups. We also attempted to obtain additional archaeological samples from the more western locations within Remote Oceania to determine as precisely as possible the mtDNA haplotypes transported into Remote Oceania.

In November 2005, the first trip to New Guinea was undertaken to trap rats and to determine if there was any evidence of Lapita on the small island of Koil, located approximately 60 km off the coast of Wewak, East Sepik Province, Papua New Guinea. If in-

deed *R. exulans* was a Lapita introduction, we would expect to find it associated with all islands that have evidence of Lapita occupation. In June and July 2006, our trapping efforts were focused on the islands in the New Ireland and Manus provinces, all of which either had known Lapita sites or were likely sites for Lapita settlement. Rats were trapped on New Ireland, Lihir, Tatau and Simberi islands in the Tabar Group, New Hanover, and Manus. We returned to New Guinea in April 2007 to trap rats and conduct archaeological excavations on Emirau (sometimes also referred to as Emira) Island in the St. Matthias Group. We were also able to arrange for a local fisherman to distribute traps and 2 ml tubes of ethanol to nearby Tench Island. We requested that local villages simply remove a small section of the tail of any rats trapped and preserve them in the tubes until the samples were collected at a later date.

MATERIALS AND METHODS

Rats were trapped using snap-type rattraps (Victor). Various volunteers from the local communities were recruited to set traps in their gardens and around the villages. Rats were brought back to the field base in the early morning, and all samples were measured, recording body length, tail length, hind foot length, maximum ear length, and nipple number. Tentative species identifications were made in the field based on morphological characteristics as described by Cunningham and Moors (1983) and Matisoo-Smith and Allen (2001). A range of tissue samples was collected from each animal, and the samples were stored in 70% ethanol to be transported to the laboratories at the University of Auckland.

DNA was extracted from tail, liver, paw, and/or ear tissue in the modern DNA Laboratory at the Department of Anthropology, University of Auckland. A preparation kit (Roche's High Pure PCR Template Preparation Kit, Roche Applied Science, Switzerland) was used according to the manufacturer's protocol for isolation of nucleic acids from mammalian tissue. To generate genetic information capable of revealing phylogenetic

structure within the species, the hypervariable control region (D-loop) of mitochondrial DNA was targeted for analysis. Primers used for amplification of a 583 base pair (bp) segment from position 15358 to 15940 (based on numbering according to Gadaleta et al. [1989]) were EGL4L (5'-CCA CCA TCA ACA CCC AAA G-3') and RJ3R (5'-CAT GCC TTG ACG GCT ATG TTG-3'). Polymerase chain reaction (PCR) amplifications were carried out in standard 30 µL reactions in which 1 µL genomic DNA was added to a reaction mixture containing 50 mM KCl, 10 mM Tris HCl pH 8.3 (10 × buffer), 2 mM MgCl₂, 150 µM dNTPs, 0.5 µM of each primer, and 0.5 U Taq-Polymerase (Ampli-Taq, Applied Biosystems). PCR was performed in a thermal cycler (iCycler, Bio-Rad Laboratories, California) with a thermal profile of 35 cycles of denaturation at 94°C for 30 sec, annealing at 60°C for 30 sec, and extension at 72°C for 1 min, preceded by an initial denaturation at 94°C for 2 min and followed by a final extension for 5 min at 72°C. Negative controls were always included to check for contamination. For verification of successful amplification, 5 µL of PCR product was visualized in ethidium bromide-stained 1% agarose gels. All PCR products were purified (QIAquick PCR Purification Kit, QIAgen, Hilden, Germany) and quantified in comparison with a low mass ladder in ethidium bromide-stained 1% agarose gels. Cycle sequencing thereafter was carried out at the Allan Wilson Centre Genome Service at Massey University, Albany, New Zealand, using a sequencing kit (BigDye Terminator v 3.1 Cycle Sequencing Kit, Applied Biosystems, Foster City, California) with 10 ng template per microliter and 1 µL 5 µM primer. Capillary separation was carried out on a genetic analyzer (ABI3730, Applied Biosystems, Foster City, California).

For identification of rat species, the sequences thus obtained were compared against the D-loop reference sequence alignment of the DNA Surveillance phylogenetic tool “What rat is that?” (www.dna-surveillance.auckland.ac.nz) using the simple cluster search (Ross et al. 2003, Ross and Murugan 2006, Robins et al. 2007).

TABLE 1
Rattus Species Recovered in Near Oceania

Location	n	R.	R.	R.	R.
		<i>exulans</i>	<i>tanezumi</i>	<i>rattus</i>	<i>norvegicus</i>
Koil Island	21	0	21	0	0
New Ireland	4	4	0	0	0
Lihir	4	3	0	1	0
Tatau	25	9	16	0	0
Simberi	2	2	0	0	0
New Hanover	9	9	0	0	0
Manus	7	5	1	0	1
Emirau	18	17	0	1	0
Tench	8	8	0	0	0
Total	98	57	38	2	1

Note: All species identified based on morphological and mtDNA analyses.

RESULTS

Trapping during the three field seasons resulted in the collection of 98 rats. The specifics regarding numbers caught, locations, and species are shown in Table 1. In his review of New Guinea mammals, Flannery (1995) had no record of *Rattus* species present on Koil, New Hanover (Lavongai), Lihir, the Tabar Group, Emirau, or Tench. Of the locations included in our study, Flannery recorded *Rattus* species only on Manus and New Ireland, with Manus having three species (*R. exulans*, *R. praetor*, and *R. rattus*) and New Ireland only two species (*R. exulans* and *R. praetor*).

A total of 57 *R. exulans* were caught in our study, and the species was present on all islands we visited except for Koil Island. All 21 rats trapped on Koil were identified by their mtDNA as *Rattus tanezumi*, an Asian rat commonly referred to as the “Asian house rat” and formerly considered a subspecies of *R. rattus* (Musser and Carleton 2005). *Rattus tanezumi* was also abundant on Tatau Island and was present on Manus. We have also previously identified it on the mainland of New Guinea (E.M.-S., unpubl. data).

We did not trap or encounter any New Guinea native rats on the islands we visited. We were also surprised to find that we trapped very few European rats, given the substantial number of U.S. military ships in

the region during World War II. We found only two *R. rattus* in our collections: one from Lihir and one from Emirau. Only one *R. norvegicus* was trapped on any of the islands we visited. This was most likely because our trapping focused on villages and in gardens rather than in larger port cities/towns where *R. rattus* and *R. norvegicus* are most likely to be found. It is not surprising that the only *R. norvegicus* was trapped in Lorengau, the main town on Manus and an administrative base for both the Japanese and the U.S./Australian forces during World War II.

Of the *R. exulans* obtained in our field study, we found that populations from New Ireland, Lihir, Tatau, Simberi, and Emirau contained lineages belonging exclusively to mtDNA Haplogroup II, also referred to in Matisoo-Smith and Robins (2004) as the Near Oceanic Type (Figure 2). We did, however, find the Remote Oceanic lineages, or

those belonging to Haplogroup III, on Tench, Manus, and New Hanover. All *R. exulans* trapped on Tench and Manus belonged to Haplogroup III, but those trapped on New Hanover belonged to both Haplogroups II and III.

DISCUSSION

The main point of the rat trapping study in the Bismarck Archipelago was to address the question regarding the apparent discontinuity between the *R. exulans* populations in Near and Remote Oceania. Is there a real difference between the two regions or is the apparent lack of connection merely the result of a sampling problem in Near Oceania? In this regard, perhaps the most important finding of our study is that we have now shown that the lack of Remote Oceanic lineages in Near Oceania was indeed due to sampling error.

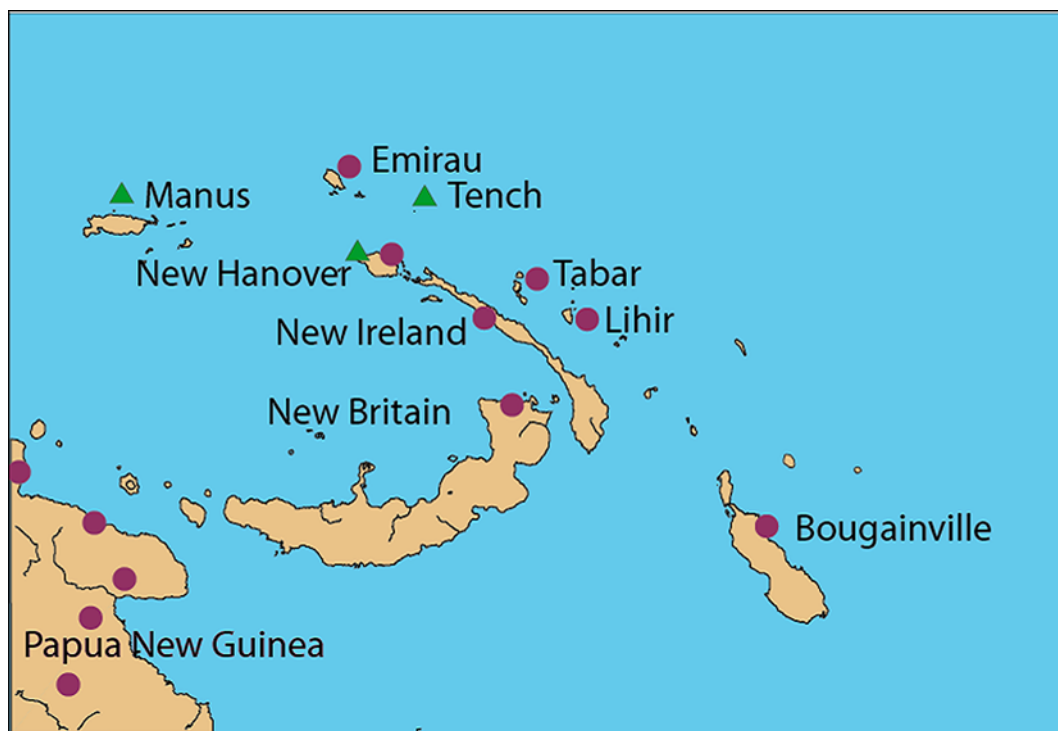


FIGURE 2. Distribution of *R. exulans* haplotypes in Near Oceania. Circles represent locations with *R. exulans* Haplogroup II lineages, and triangles represent locations with Haplogroup III lineages.

There is now a clear connection between the *R. exulans* populations found in Remote Oceania and those found in the Bismarck Archipelago and a path linking the Remote Oceanic rats back to the island of Halmahera in the Moluccas, the most westerly location in which we have found Haplogroup III.

It is tempting, given the near-ubiquitous distribution of Haplogroup III in Remote Oceania and its now-known distribution in the Bismarck Archipelago, to suggest that Haplogroup III *R. exulans* is indeed a marker of Lapita migration. The presence of Haplogroup III *R. exulans* on Manus is also interesting given that island's importance in the Lapita-associated obsidian exchange system (Spriggs 1997, White and Harris 1997, Summerhayes 2003). However, if we consider the known distribution of early Lapita sites in the Bismarck Archipelago, we find that the majority of those islands sampled so far have *R. exulans* belonging exclusively to Haplogroup II—these include New Ireland and adjacent islands, New Britain, and Emirau—located just a few kilometers from Mussau and the location of some of the earliest dated Lapita deposits (Kirch 2000, Summerhayes 2007). The Ererae archaeological site, located during our time on Emirau, has now been securely dated and represents one of the earliest Lapita sites (G.S., E.M.-S., J. Specht, K. Amanga, K. Thomas, and J. Ridges, unpubl. data). It is interesting that the one location in Near Oceania in which we previously identified Haplotype II was the Reef/Santa Cruz islands, just over the boundary between Near and Remote Oceania (Matisoo-Smith and Robins 2004). The sample consisted of a bone recovered from the SE-RF-3 site, and although the site is clearly post-Lapita (and therefore, again, does not provide any direct association between Lapita and Haplotype II), there is archaeological, linguistic, and genetic evidence for direct Lapita as well as post-Lapita links between the Reef/Santa Cruz islands and the Bismarck Archipelago (Green 1997, Friedlaender *et al.* 2002, Sheppard and Walter 2006, Ross and Naess 2007).

Unfortunately our preliminary test excavations of the Ererae site did not result in the recovery of any faunal remains other than

fishbone, so we cannot yet be sure that the Haplotype II *R. exulans* we found on Emirau represents an introduction by the first Lapita colonists. However, given the relatively close association between Lapita settlements and the appearance of *R. exulans*, coupled with the fact that there is no indication of a pre-Lapita settlement phase on the island, we suggest that, at least in Near Oceania, Lapita settlement was associated with both Haplogroups II and III. The fact that very few island populations actually have both haplogroups may indicate that there were two Lapita introductions of *R. exulans* to Near Oceania, with the earliest arrivals bringing Haplogroup II.

The introduction of Haplogroup III into Near Oceania and its dispersal into and throughout Remote Oceania may be associated with a slightly later or additional group of Lapita colonists. Alternatively, the predominance of one haplogroup over another on the islands could be the result of genetic drift or bottlenecks. Only analyses of archaeological *R. exulans* remains can resolve this question. We are currently planning further archaeological excavations of Lapita sites or closely associated natural deposits in the region to recover *R. exulans* bones for aDNA analyses to address this issue.

One island on which we did find the Remote Oceanic, Haplogroup III, *R. exulans* that does not yet have any indication of Lapita settlement is Tench Island. Tench is a small, isolated atoll in the St. Matthias Group and is located approximately 70 km east of Emirau. Unlike Emirau Island, Tench is only a few meters above current mean sea level and would have been submerged during the mid-Holocene high sea stand (*i.e.*, the period of Lapita occupation). As on Emirau and Mussau, the current populations had historic connections with the eastern Carolines in Micronesia to the north, and this can be seen today in the presence of backstrap weaving loom, which was a Micronesian introduction (see Parkinson 1999:143, 148). Yet Tench was culturally isolated from both Emirau and Mussau to the west, and *R. exulans* on Tench may well have been introduced from Micronesia to the north.

The only island on which we trapped but did not find any *R. exulans* was Koil, located some 60 km off the north New Guinea coastline. The island is composed of raised limestone, some 4 km long and only 2 km at its widest point. The archaeological survey and test pitting on Koil Island (G.S., M. Leavesley, A. Fairbairn, and G. Hope, unpubl. data) indicated that there was also no evidence of Lapita settlement on the island, with permanent settlement probably no earlier than 600 years in age (G.S., M. Leavesley, A. Fairbairn, and G. Hope, unpubl. data). This result adds strength to the argument that *R. exulans* was dispersed primarily, if not exclusively, by Lapita peoples in Near Oceania.

In addition to trapping *R. exulans*, we also encountered a number of other *Rattus* species that were introduced to the islands we visited. These introduced species not only impact the distribution of *R. exulans*, but also New Guinea native species. We have no idea how long *R. tanezumi* (sometimes referred to as *Rattus rattus mansorius*) has been in New Guinea or on the islands of Near Oceania, but it is clearly not a native species to New Guinea (Musser and Carleton 2005). Flannery (1995) suggested that it is a relatively recent introduction to the region. It is present in much of western Micronesia, where it predates the appearance of *R. exulans* in the archaeological record (Wickler 2004).

The fact that we trapped no New Guinea native rats on any of the islands was surprising. Flannery (1995) recorded that *R. praetor* is/was present on New Ireland, Manus, and Blup Blup, an island located quite close to Koil within the Schouten Group. Another New Guinea rodent, *Melomys rufescens*, believed to be native to New Ireland, is also recorded on Blup Blup. Flannery (1995:145) stated that *Melomys rufescens* is "a very common species, particularly in disturbed habitats throughout its range. It is often found in houses, particularly where introduced murids are rare or absent, and it can often be seen climbing in low vegetation in gardens or near villages at night." This is exactly where and when we were trapping, so the fact that we did not encounter any *Melomys* on New Ireland or Koil, and no *R. praetor* on New

Ireland, Manus, or Koil, may indicate that the distribution of both of these species is now being impacted by more recently introduced species.

CONCLUSIONS

Our focused sampling of *Rattus* species on the islands of Near Oceania has solved one mystery identified by our previous genetic analyses of *R. exulans* as a proxy for tracking human migrations. Although we now have evidence of *R. exulans* Haplogroup III in Near Oceania and thus no major discontinuity between Near and Remote Oceanic *R. exulans* populations, it now appears that we may have more than one *R. exulans* lineage associated with Lapita dispersal.

The distribution of *R. exulans* Haplogroup II does appear to be associated with islands associated with early Lapita colonization in Near Oceania. Whether these rats were in the region before the arrival of Lapita is not yet clear. Haplogroup III, however, was clearly the main lineage taken out to most of Remote Oceania. Because there is no way of identifying morphologically which rats carry which mtDNA lineage, intentional human selection is unlikely to have determined which haplotypes were transported. The distribution does suggest that the source population for the settlement of Remote Oceania must have come from a location where Haplogroup III was present, if not the predominant lineage. Does this then suggest two Lapita dispersals, with the first arrivals in Near Oceania carrying Haplogroup II rats, dispersing perhaps as far as the Reef/Santa Cruz islands and possibly northern Vanuatu, and later arrivals heading out farther east through Remote Oceania carrying Haplogroup III *R. exulans*? Clearly only aDNA analyses of well-dated archaeological rat remains will solve this question.

Unfortunately, to date, we do not have many archaeological collections in Near Oceania that include large numbers of rat bones and date between 3,000 and 4,000 B.P. Unless we can find rat bones in well-protected sites such as rock shelters or caves, our chances of being able to obtain DNA from

those 3,000+ year old faunal remains using traditional DNA techniques are not high because of DNA degradation in tropical climates (Robins et al. 2001). However, we are continuing to look for such archaeological samples, and recent developments in DNA sequencing technology may provide the tools to obtain reliable DNA sequences from highly degraded samples (Millar et al. 2008).

The results of this study combined with those of our previous work show the potential for using commensal animals to address issues of Pacific prehistory. Given that at least two other rat species were introduced and transported through Near and Remote Oceania during prehistory, analyses of *R. praetor* and *R. tanezum*i can perhaps provide further evidence of human mobility and migration in the region. In addition, analyses of the other commensal animals, including not only those associated with Lapita expansion, but also those moved to islands by earlier inhabitants of Near Oceania, could also be valuable. All of these future studies of commensal plants and animals, however, need to be conducted carefully with full cooperation and collaboration between archaeologists, faunal experts, and biologists to fully interpret and make the most of the resulting data. In addition, we need good chronological control based on analyses of well-dated archaeological remains as well as extant samples to fully understand the biogeography and genetic variation of commensal animals and how that relates to past human behavior.

ACKNOWLEDGMENTS

We acknowledge and thank the following people who assisted with collections and made the fieldwork possible, not to mention enjoyable: Herman Mandui, Geoff Hope, Andy Fairbairn, Jim Specht; Chief Matthew and the people of Wanap village on Koil Island; Jimmy Peter, Andy Holding, and Lihir Gold on Lihir; Ken, King, Elsie, Jessie, Selina, Dennis, and all at Andi's Guest House on Tatau; Bernard Minol and family, Father Paul Mohe, and the congregation of Lorengau Catholic Church on Manus; Shawn Yip, John Aini, and Jim Ridges on New Ireland;

and Kelly Amanga, Kenneth Thomas, Pastor Wilson, and the staff and students at Rongoe School on Emirau.

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